

The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California

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Summary

1 We assess the use of simple, size-based matrix population models for projecting population trends for six coniferous tree species in the Sierra Nevada, California. We used demographic data from 16 673 trees in 15 permanent plots to create 17 separate time-invariant, density-independent population projection models, and determined differences between trends projected from initial surveys with a 5-year interval and observed data during two subsequent 5-year time steps.

2 We detected departures from the assumptions of the matrix modelling approach in terms of strong growth autocorrelations. We also found evidence of observation errors for measurements of tree growth and, to a more limited degree, recruitment. Loglinear analysis provided evidence of significant temporal variation in demographic rates for only two of the 17 populations.

3 Total population sizes were strongly predicted by model projections, although population dynamics were dominated by carryover from the previous 5-year time step (i.e. there were few cases of recruitment or death). Fractional changes to overall population sizes were less well predicted. Compared with a null model and a simple demographic model lacking size structure, matrix model projections were better able to predict total population sizes, although the differences were not statistically significant. Matrix model projections were also able to predict short-term rates of survival, growth and recruitment. Mortality frequencies were not well predicted.

4 Our results suggest that simple size-structured models can accurately project future short-term changes for some tree populations. However, not all populations were well predicted and these simple models would probably become more inaccurate over longer projection intervals. The predictive ability of these models would also be limited by disturbance or other events that destabilize demographic rates.

Key-words: growth autocorrelation, matrix models, population projections, size structure, tree demography

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Introduction

Structured population models are basic tools for analysing demographic data. An important, but contentious, application of this method is projecting future population behaviour from observed conditions. Models can only project future population trends accurately if their structure and data quality are reliable descriptors of the populations concerned. Data quality issues have received considerable attention, particularly in terms of errors and biases in sampling (Ludwig

1999; Fieberg & Ellner 2000; Meir & Fagan 2000). Adequate models may need to include complex or data-intensive features, such as cryptic demographic stages (Kalisz & McPeck 1992), periodic environments (Beissinger 1995), ecological interactions (e.g. density dependence, meta-population dynamics) (Alvarez-Buylla 1994; Lindenmayer *et al.* 2000) and temporal/spatial fluctuations in demographic rates [Horvitz & Schemske 1995 (but see Caswell 2001); Bierzychudek 1999]. More fundamentally, Pfister & Stevens (2003) have demonstrated by simulation that species with strong growth autocorrelations (i.e. growth rates that are non-randomly distributed among individuals over time) violate the assumptions of most size-structured

population models, which may result in biased projections.

Trees are some of the best studied long-lived perennial plants, but possess life history traits that impede the creation of structured population models. Demographic processes occur slowly for most tree species, requiring large sample sizes and long observation intervals to estimate vital rates. It is also unclear how tree size affects individual fates. It is generally assumed that individual tree reproduction and growth tend to be positively size-dependent (Harper 1977; Pacala *et al.* 1994), whereas mortality probabilities decrease with tree size (Hawkes 2000). However, empirical evidence questions whether growth and mortality are strongly size-dependent (Clark & Clark 1999; our unpublished data). Demographic rates are also thought to be shaped by patch scale interactions, which could result in strong growth autocorrelations. The use of individual-based forest 'gap' models (Bugmann 2001) is an attempt to account explicitly for localized environmental differences. However, demographic rates for tree populations are likely to change slowly in the absence of disturbance, suggesting that it may be possible to create accurate projections, and several researchers have used size-structured population models to project demographic trends of trees (Olmsted & Alvarez-Buylla 1995; Schwartz *et al.* 2000; Kohira & Ninomiya 2003; Kwit *et al.* 2004; Lytle & Merritt 2004). The meta-analytical approach of Brook *et al.* (2000) has not been attempted for plants, and it is unclear whether simple tree population models are useful for predicting demographic trends.

We assess the accuracy of projections from 17 separate simple, deterministic, size-structured population models using long-term demographic data for six coniferous tree species at several sites in the Sierra Nevada, California. We record demographic changes between the beginning and end of an initial 5-year period and use these data to determine differences between projected and observed population trends in subsequent 5-year time steps. We address the question of whether simple matrix models can be used to describe these populations and if there are significant or systematic differences between the projected and actual future demographic trends in our tree populations over short periods of time. If short-term projections fail, longer-term projections are unlikely to be successful.

Methods

Permanent study plots were established in the coniferous forest belts of Sequoia and Yosemite National Parks in the Sierra Nevada of California (Table 1). The sites have never been logged. The climate is mediterranean, with hot, dry summers and cool, wet winters, with about half of the annual precipitation falling as snow (Stephenson 1988). Average January and July air temperatures are roughly 2 °C and 19 °C, respectively (Major 1977). Frequent fires characterized

Sierran forests prior to European settlement, but the areas containing the study plots have not burned since the late 1800s (Swetnam *et al.* 1992).

In each plot all trees ≥ 1.37 m in height were tagged, mapped, measured for diameter and identified to species level. We performed mortality assessments annually starting at the time the plots were established. Trees were recorded as dead only if they showed complete needle browning or loss. We continued to track dead trees for as long as we were able to relocate the stems to ensure a correct judgement of tree death. We took measurements of live tree stem diameter at breast height (d.b.h. 1.37 m), with breast height marked with a nail for precise relocation. We measured tree diameters typically at 5-year intervals, and calculated radial growth from these repeated measurements. During the measurement years new trees (ingrowth reaching 1.37 m) were recorded as recruitment. Analysis was limited to the numerically dominant species within each forest type, which included *Abies concolor* (Gordon & Glend.) Lindley, *A. magnifica* s.l., *Calocedrus decurrens* (Torrey) Florin, *Pinus jeffreyi* Grev. & Balf., *P. lambertiana* Doug. and *P. ponderosa* Laws. *Abies* spp. and *C. decurrens* are shade tolerant whereas the *Pinus* species are moderately to robustly shade intolerant (Minore 1979). We were interested in temporal patterns in the data, so we excluded individual trees that had missing data during any measurement year. This resulted in the removal of 100 trees, leaving 16 673 trees for demographic analysis. Three time steps (0–5, 5–10 and 10–15 years) were analysed.

We organized demographic data for the first 5-year interval as time-invariant, density-independent, size-structured population models with 5-year time steps. We created five stem diameter classes (0.0–5.0, 5.1–10.0, 10.1–20.0, 20.1–40.0, > 40.0 cm d.b.h.), which roughly correspond to canopy position (i.e. sapling, understory, intermediate, co-dominant, dominant) (N. Stephenson unpublished data). No backward transitions or skipping size classes were permitted. Frequencies of mortality and growth to larger size classes were taken directly from field observations. We did not measure the fecundity of individual trees. Lacking fecundity data, we estimated reproductive output from recruitment of new trees (as defined above), with the assumption that only trees > 40 cm d.b.h. contributed to recruitment. This relatively crude assumption is based on the results of Fowells & Schubert (1956), who recorded only small amounts of cone production for trees < 40 cm d.b.h. for *A. concolor*, *P. lambertiana* and *P. ponderosa*. Size-specific reproductive data were not available for *A. magnifica*, *C. decurrens* and *P. jeffreyi*, but the majority of cone production occurs in the largest trees (Jenkinson 1990; our personal observations). Seeds are not stored in long-term seedbanks, and none of these species reproduces vegetatively. The 5-year resolution of our growth and recruitment data provides an adequate observation length to measure demographic rates for these trees. Population projections were likewise

Table 1 Characteristics of permanent forest plots. Species names presented in bold were used for analysis

Population name	Plot name	Measurement years	Elev. (m)	Plot size (ha)	Stem count*	Species composition†
Hodgedon Meadows	YOHPIPO	1991, 1996, 2001	1500	1.0	2978	ABCO 35%; CADE 32%; PILA 26%; PIPO 5%; PSME 1%; QUKE 1%
	Crane Creek	1993, 1998, 2003	1637	1.0	1752	ABCO 44%; CADE 29%; PILA 19%; PIPO 6%; QUKE 2%
Crystal Road	BBBPIPO	1992, 1997, 2002	1609	1.0	1273	CADE 55%; QUKE 24%; ABCO 12%; PILA 5%; PIPO 4%; QUCH 1%
	CCRPIPO	1991, 1996, 2001	1637	1.1	2102	ABCO 46%; CADE 30%; QUKE 15%; PILA 5%; PIPO 4%
Suwanee Creek	SuwCreek	1983, 1988, 1994, 1999	2033	1.4	1026	ABCO 55%; CADE 20%; PILA 20%; ABMA 4%; QUKE 1%
	SuwABCO	1983, 1988, 1994, 1999	2035	0.9	680	ABCO 59%; CADE 28%; PILA 9%; ABMA 4%
	SuwPILA	1983, 1988, 1994, 1999	2059	1.1	765	ABCO 68%; PILA 21%; CADE 9%; QUKE 1%
SEGI Conifer	LMCC	1982, 1988, 1994, 1999	2128	2.0	672	ABCO 71%; ABMA 20%; SEGI 7%; PILA 2%
	LogSEGI	1983, 1988, 1994, 1999	2170	2.5	1055	ABCO 76%; ABMA 15%; PILA 5%; SEGI 3%
Log Creek	LogABCO	1987, 1992, 1997, 2002	2207	1.1	458	ABCO 75%; ABMA 22%; PILA 2%; SEGI 1%
	LogPILA	1987, 1992, 1997, 2002	2210	1.0	434	ABCO 90%; PILA 6%; CADE 2%; PIJE 1%; QUKE 1%
Xeric Conifer	FrPIJE	1983, 1988, 1994, 1999	2106	1.0	178	PIJE 79%; QUKE 9%; ABCO 7%; PILA 2%; CADE 2%; PIMO 1%
	LogPIJE	1985, 1990, 1995, 2000	2405	1.0	121	ABCO 59%; PIJE 39%; ABMA 2%; PILA 1%
Tuolumne River	SftrABMA	1992, 1997, 2002	2484	1.0	1631	ABMA 100%
Panther Gap	PgABMA	1992, 1997, 2002	2576	1.0	765	ABMA 100%

*Stems defined as individuals ≥ 1.37 m tall at time of plot establishment.

†Species composition of all stems at time of plot establishment. Percentages may not add to 100 due to rounding. **ABCO** = *Abies concolor*, **ABMA** = *A. magnifica*, **CADE** = *Calocedrus decurrens*, **PIJE** = *Pinus jeffreyi*, **PILA** = *P. lambertiana*, **PIPO** = *P. ponderosa*, **PIMO** = *P. monticola*, **PSME** = *Pseudotsuga menziesii*, **QUCH** = *Quercus chrysolepis*, **QUKE** = *Q. kelloggii*, **SEGI** = *Sequoiadendron giganteum*.

calculated at 5-year intervals. Occasionally the growth and reproduction measurements were taken on a 6-year interval; we standardized these data to a 5-year interval to calculate transition probabilities.

In most cases we grouped plots that shared geographical proximity and similar elevations to estimate transition probabilities (distance among grouped plots, average = 2.9 km, range = 0–10.2 km), because Stephenson & van Mantgem (in press) show that plots with similar elevations share similar demographic rates. We considered individual plots, or plot groups where we could create independent models, to be populations (Table 1). For some populations there were no observations of certain stage transitions, despite the fact that, although rare, they must occur (typically mortality for trees > 40 cm d.b.h.). We left these probabilities at their observed rate of 0, although this might translate into inaccurate projections at longer time intervals. The size-structured projection models took the form $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where $\mathbf{n}(t)$ is a vector of the stage abundances at time t , and \mathbf{A} is the matrix containing transition probabilities that describe the contribution of each stage to the population at the next time step. Population matrices and asymptotic growth rates (λ) for the initial 5-year interval are given in Appendix 1, which is available as supplementary material.

We checked for observation errors and violations of the assumptions of matrix models. The 5-year interval means that we may have missed newly recruited trees that grew to 1.37 m and died before being counted (hereafter called 'ghost mortalities'). However, we recorded recruitment annually from 1999, and found little evidence of widespread ghost mortalities (proportion of recruits from 1999 to 2003 that died between 2000 and 2003: *A. concolor* 2%, *A. magnifica* 2%, *C. decurrens* 1%, *P. jeffreyi* 0%, *P. lambertiana* 7%, *P. ponderosa* 0%).

We followed the methods of Pfister & Stevens (2002) to measure growth autocorrelations. We evaluated size-dependent growth by assessing the effect of tree diameter on subsequent radial growth with linear regression using a quadratic model during two 5-year intervals, and compared the residuals from the two time intervals. Our quadratic model was $G_{t+1} = C + \alpha_1 \cdot \text{DBH}_t + \alpha_2 \cdot \text{DBH}_t^2$, where G_{t+1} is the radial growth rate at the second time step and DBH_t is the stem diameter at the first time step. Growth autocorrelations were considered to be present if there was a positive and significant relationship between the two. To compare our results directly against the findings of Pfister & Stevens (2003) we considered, simultaneously, the effects on growth of previous growth and size, using multiple regression ($G_{t+1} = C + \alpha \cdot \text{DBH}_t + \beta \cdot G_t$, corresponding to equation 1 in Pfister & Stevens 2002), for stems < 40 cm d.b.h. where we do not find a curvilinear response between stem diameter and radial growth (see Fig. 1).

Our growth measurements yielded negative growth rates for 8.1% of trees on average over the three 5-year

intervals analysed. Negative growth rates probably arose from measurement error, transcription error or bark loss between measurements. Trees with negative growth rates were retained to avoid biasing our growth analyses in favour of trees with growth rate errors in the positive direction, which we had no way of identifying. However, we wished to remove outliers with exceptionally large positive and negative growth rates, which had a disproportionate influence on growth statistics. Data from cores and complete cross-sections from about 400 trees of all species in the montane forests of Sequoia National Park (N. Stephenson unpublished data) indicated that the actual maximum radial growth rate for a tree was unlikely to be > 8 mm yr⁻¹. We chose 1 mm yr⁻¹ as the largest acceptable error in growth rate, and because actual minimum growth rate could not be < 0 mm yr⁻¹, we used trees with growth rates of -1 mm yr⁻¹ to 9 mm yr⁻¹ for our growth analyses. An average of 3.0% of trees during each 5-year interval fell outside this range. These trees were dropped from the analysis of size-dependent growth and growth autocorrelations, leaving 11 591 individual trees for the comparison of years 0–5 and 5–10, and 3863 individual trees for the years 5–10 and 10–15. Trees with extreme growth rates were not excluded from building the population matrices.

We used loglinear analyses to detect temporal and spatial variations in transition probabilities for our populations (Horvitz & Schemske 1995; Caswell 2001). Our loglinear analyses considered the dependence of an individual's fate (F , five size classes at $t+1$ and death) on the independent variables of initial state (S , the five size classes at t), time (T , years 0–5, 5–10) and locations (L , spatial differences among populations where we had multiple populations of the same species). The null model contains the interaction of the explanatory variables and assumes that the size class variables influence fate (STL , SF). Additional models consider the interactions between fate and time (STL , SFT), the interactions between fate and location (STL , SFL), and the additive effects of the time and location interactions (STL , SFT , SFL). These models are compared against the saturated model, which considers all possible interactions ($SFTL$). We selected the best model for each species using the Akaike information criterion (AIC), which is a ranking procedure defined as $\text{AIC} = G^2 - 2(\text{d.f.})$, where G^2 is the goodness-of-fit likelihood ratio statistic and d.f. is the degrees of freedom (Caswell 2001). The likelihood of a given model increases as more parameters are added, but the decreasing negative log likelihood is offset by increases in d.f. The best model has a relatively small AIC owing to the combination of a relatively large likelihood and a parsimoniously small number of parameters. Competing models are compared by scaling their AIC values against the best model with the lowest AIC value. The rescaled AIC values are written as ΔAIC . Models with $\Delta\text{AIC} = 2$ have substantial support, and fit almost equally well as the best model (Burnham &

Anderson 1998). We also tested for temporal variations alone for individual populations by comparing the saturated model *SFT* against the model *FS*, *ST*, using likelihood ratio statistics to determine significance.

Numerical projections were calculated by multiplying the observed population stage abundances with the observed transition probabilities from the years. These projections were used to calculate expected total population sizes, and the summed frequencies of survival, growth, recruitment and death for all size classes during the years 5–10 and 10–15. A property of matrix models is that projection results are expected to fluctuate until a stable stage distribution is reached. We assessed the influence of the initial observed stage distribution on our projections by calculating their distance from the stable stage distribution using Keyfitz's Δ , defined as

$$\Delta(\mathbf{x}, \mathbf{w}) = \frac{1}{2} \sum_i |x_i - w_i|$$

where \mathbf{x} and \mathbf{w} are the vectors of the observed and the stable stage distributions scaled to 1.0 (Caswell 2001). Values for Keyfitz's Δ range between 1 and 0, with smaller values being obtained as the observed and stable stage distributions become more similar. We combined the projection results from all of the models and compared them against the observed population data using linear regression. We also compared the matrix model results against two competing models: a null model of no population change [$N(t) \equiv N(0)$], and a simple population model ignoring size structure [at a 5-year interval, $N(t+5) = (b-d)N(t)$, where b and d are recruitment and death rates during the first 5-year interval]. Model results were compared using an error sum of squares [error $SS = \Sigma(X_{\text{observed}} - X_{\text{predicted}})^2$], where X_{observed} is the observed total population size and $X_{\text{predicted}}$ is the total population size predicted by a given model for an individual population. We tested if error $SS_{\text{model 1}} - \text{error } SS_{\text{model 2}} = 0$ with a paired t -test using square root transformations to normalize the data. We calculated matrix model projections using PopTools, version 2.5 (Hood 2003). We conducted statistical tests with SYSTAT, version 10.2 (SYSTAT 2002).

Results

We found evidence of size-dependent growth and growth autocorrelations for the years 0–5 and 5–10 (Figs 1 & 2). Multiple regressions of size and growth also generally found these variables to predict future growth for stems < 40 cm d.b.h. (α average and range = 0.025, 0–0.039, β average and range = 0.537, 0.414–0.663). We found similar results for the years 5–10 and 10–15, where regressions for size-dependent growth were statistically significant ($P < 0.001$) for all species, and the variation in growth explained by size for the significant relationships averaged 12%. Previous growth explained 34% of the variance on average when size–growth residuals were examined and coefficients were

Table 2 Loglinear analyses assessing the effects of time (T , years 0–5, 5–10) and location (L) on individual fate (F), given the initial stage class (S)

Model	G^2	d.f.	P	AIC	Δ AIC
<i>Abies concolor</i>					
<i>STL</i> , <i>SF</i>	385.02	225	<0.0001	–65.0	51.7
<i>STL</i> , <i>SFT</i>	353.45	200	<0.0001	–46.6	70.2
<i>STL</i> , <i>SFL</i>	133.28	125	0.2896	–116.7	0.0
<i>STL</i> , <i>SFT</i> , <i>SFL</i>	99.64	100	0.4914	–100.4	16.4
<i>SFTL</i>	0	0		0.0	116.7
<i>A. magnifica</i>					
<i>STL</i> , <i>SF</i>	358.24	175	<0.0001	8.2	140.6
<i>STL</i> , <i>SFT</i>	235.63	150	<0.0001	–64.4	68.0
<i>STL</i> , <i>SFL</i>	67.68	100	0.9945	–132.3	0.0
<i>STL</i> , <i>SFT</i> , <i>SFL</i>	38.71	75	0.9998	–111.3	21.0
<i>SFTL</i>	0	0		0.0	132.3
<i>Calocedrus decurrens</i>					
<i>STL</i> , <i>SF</i>	230.25	125	<0.0001	–19.8	26.4
<i>STL</i> , <i>SFT</i>	153.88	100	0.0004	–46.1	0.0
<i>STL</i> , <i>SFL</i>	111.04	75	0.0043	–39.0	7.2
<i>STL</i> , <i>SFT</i> , <i>SFL</i>	73.68	50	0.0163	–26.3	19.8
<i>SFTL</i>	0	0		0.0	46.1
<i>Pinus lambertiana</i>					
<i>STL</i> , <i>SF</i>	182.09	125	<0.0001	–67.9	–3.8
<i>STL</i> , <i>SFT</i>	121.22	100	0.0732	–78.8	–14.7
<i>STL</i> , <i>SFL</i>	85.89	75	0.1832	–64.1	0.0
<i>STL</i> , <i>SFT</i> , <i>SFL</i>	39.66	50	0.8525	–60.3	3.8
<i>SFTL</i>	0	0		0.0	64.1

positive and statistically significant ($P < 0.001$). Future growth was also related to past growth and stem size when considered simultaneously during this time interval for trees < 40 cm d.b.h. (α average and range = 0.016, 0–0.032, β average and range = 0.692, 0.560–0.763).

Loglinear tests found that populations of the same species were more variable across locations than time (Table 2). An exception to this was *C. decurrens*, which showed strong variation in demographic rates over time but not locations. We conducted the same tests using the two most recent observation intervals for each population to minimize potential effects of inter-annual environmental differences, but found nearly identical results. For individual populations loglinear analysis provided evidence of significant temporal variability in demographic rates for only two of 17 populations (*FS*, *ST*: Hodgedon Meadows *A. concolor* $G^2 = 38.0$, d.f. = 25, $P = 0.046$, Crystal Road *C. decurrens* $G^2 = 101.8$, d.f. = 25, $P < 0.001$). Variation in small tree (0.1–5.0 cm d.b.h.) mortalities appeared to be responsible for changes to these populations. The initial observed stage distributions were generally close to the stable stage distributions (minimum, maximum and average Keyfitz's $\Delta \pm \text{SD} = 0.054, 0.651, 0.229 \pm 0.186$). The low degree of temporal variation and similarities among observed and stable population distributions appeared to allow time-invariant model projections to follow observed total population sizes closely for both observation intervals. The projected

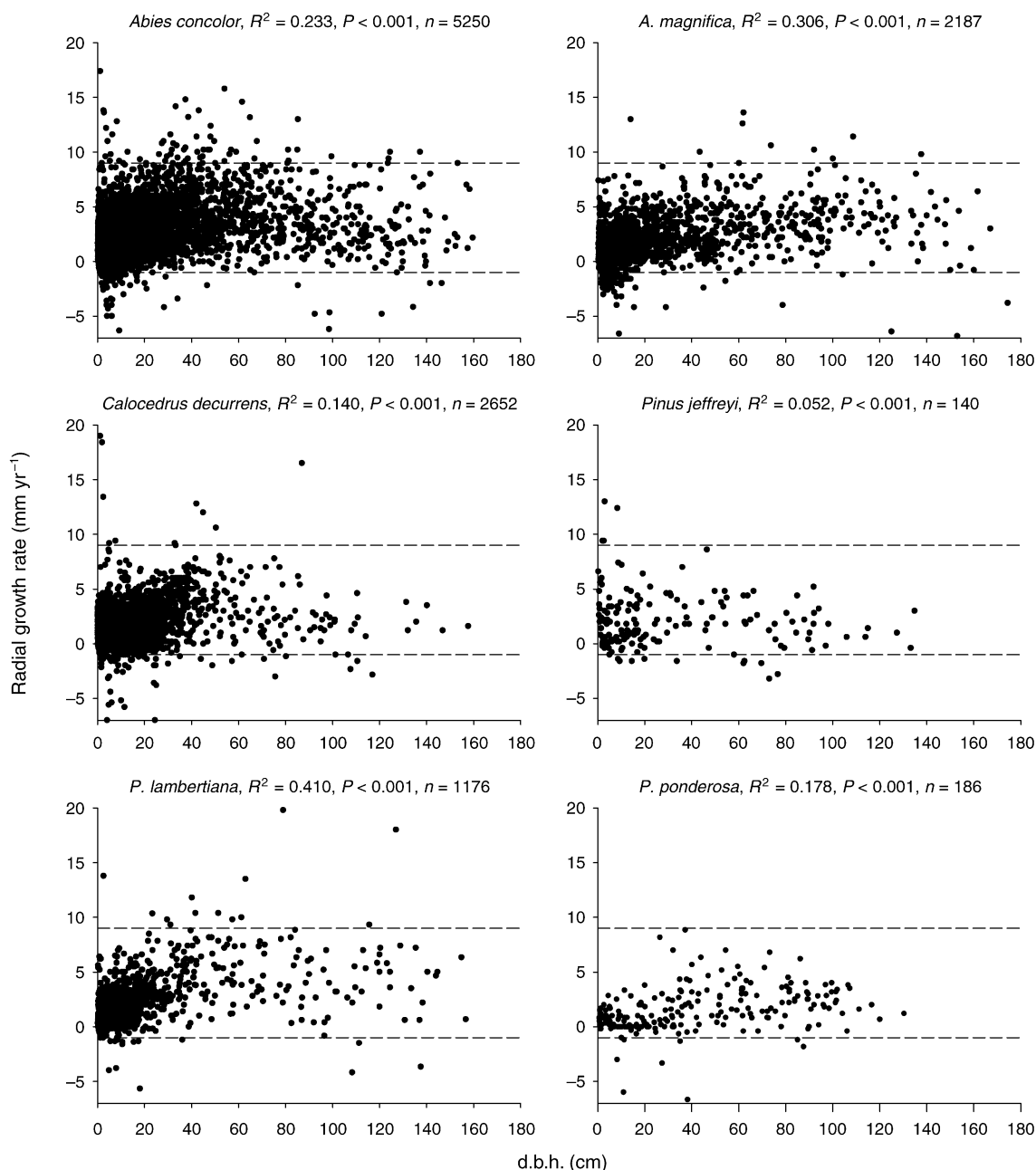


Fig. 1 Size-dependent growth for the years 0–5. We limited our regressions to trees with growth rates of -1 to 9 mm yr^{-1} (see Methods), bounded by dashed lines, to calculate the influence of stem diameter on radial growth.

stage distributions were close to the observed distributions, with significant differences found only in the Crystal Road *C. decurrens* population at year 10 ($G^2 = 27.3$, d.f. = 4, $P < 0.001$) where recruitment was greater than expected, and the Log Creek *A. magnifica* population at year 15 ($G^2 = 12.4$, d.f. = 4, $P = 0.015$) where deaths were more infrequent than expected.

Combining the model results, we found the amount of variation that the regression models of total populations could explain was high (year 10, $R^2 = 0.988$, $P < 0.0001$; year 15, $R^2 = 0.989$, $P < 0.0001$). There were, however, only low levels of recruitment and mortality so the total population sizes were strongly correlated among time steps. Fractional changes to total population sizes from year 5 to years 10 and 15 show

that most projections models account for the observed changes, but with notable exceptions (Fig. 3). Whereas the regression model results were non-significant (year 10, $P = 0.153$; year 15, $P = 0.734$), removal of the Log Creek *A. magnifica* population allowed the combined model results to follow observed trends more closely (year 10, $R^2 = 0.455$, $P = 0.004$, intercept 95% CI = -1.08 to 0.50 , slope 95% CI = 0.48 – 2.09 ; year 15, $R^2 = 0.577$, $P = 0.048$, intercept 95% CI = -2.12 to 0.91 , slope 95% CI = 0.03 – 3.11).

Alternative models were also able to predict total population sizes due to the large effect of population carryover. Comparing the error SS of the models showed a closer agreement between the matrix models vs. the other population models, although these differences

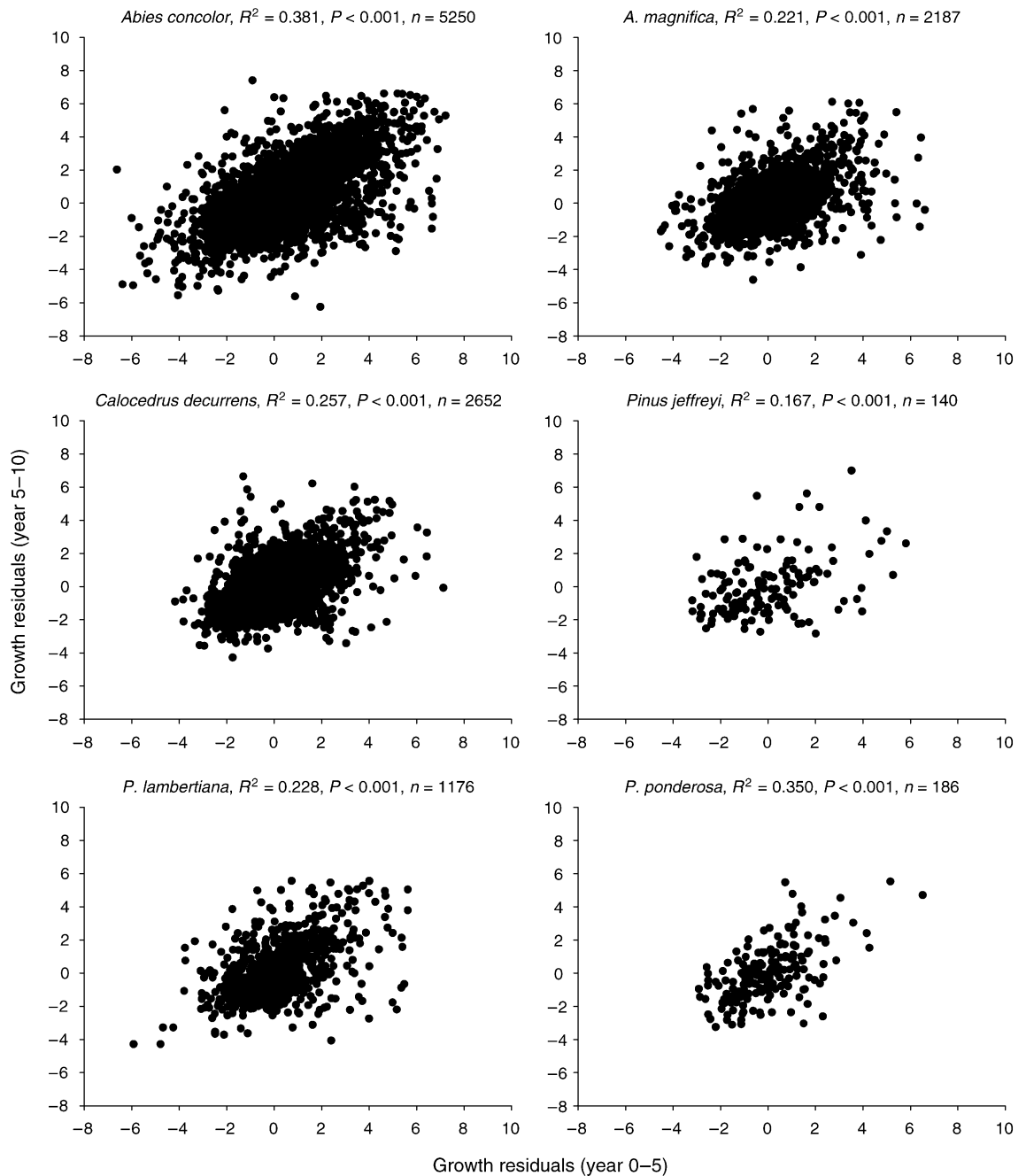


Fig. 2 Growth autocorrelations for the years 0–5 and 5–10. The range of radial growth rates used to calculate temporal correlations in growth was limited to -1 to 9 mm yr^{-1} (see Methods).

were not statistically significant [years 5–10, mean square error (MSE_{Null}) = 7273, $\text{MSE}_{\text{Unstructured}}$ = 4462, $\text{MSE}_{\text{Matrix}}$ = 3860, paired $t \geq 0.16$, d.f. = 16, $P \geq 0.09$; years 10–15, MSE_{Null} = 5839, $\text{MSE}_{\text{Unstructured}}$ = 3720, $\text{MSE}_{\text{Matrix}}$ = 3456, paired $t \geq 0.01$, d.f. = 7, $P \geq 0.73$]. Regression models of fractional changes to total population sizes also showed poorer fits for the null and unstructured models compared with the matrix models.

There was general agreement among matrix model projections and the observed frequencies of survival, growth and recruitment for the interval 5–10 years (Fig. 4). Death rates were not well predicted during this observation interval. The 95% confidence intervals for

the intercept and slope parameters overlapped 0.0 and 1.0, respectively, for the regression models of survival and recruitment. The Log Creek *A. magnifica* had a higher than expected frequency of growth, which resulted in model misspecifications (intercept 95% CI = 0.005–0.057, slope 95% CI = 0.251–0.881). Removal of this observation resulted in intercept and slope parameters overlapping 0.0 and 1.0, respectively. Regressions of matrix model predictions of demographic rates were not statistically significant for the interval 10–15 years, although the survival, growth and recruitment coefficients for the intercept were close to zero (range 0.038–0.259), and the slope coefficients were positive (range 0.115–0.710). Similar results were obtained for years 5–10 and

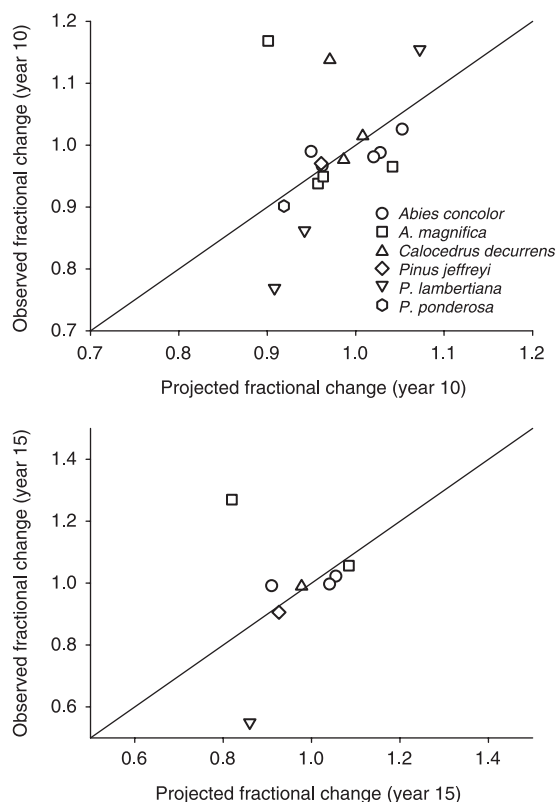


Fig. 3 Projected vs. observed fractional change in total population sizes from year 5 to year 10 ($n = 17$) and year 15 ($n = 8$). The solid line at 45° indicates perfect agreement between projected and observed fractional population sizes. Note different scales are used for years 10 and 15.

10–15 using the unstructured model to predict rates of survival, recruitment and death.

Discussion

Our results indicate that simple size-structured models were generally useful for predicting total population sizes and some demographic rates over short time horizons for the tree species we considered. We found evidence of observation errors for the growth and recruitment data (i.e. negative growth rates and ghost mortalities). The mortality data probably contained an inconsequential amount of observation error, as tree death is easy to detect and was rechecked annually. We detected violations of the assumptions of structured population models, especially with respect to growth autocorrelations. The simulation results of Pfister & Stevens (2003) indicate that growth autocorrelations should have a large effect on matrix projections only when coupled with strong positive size-dependent growth (i.e. $\alpha = 0.03$ and $\beta = 0.8$), which could be problematic for our projections. However, errors associated with growth autocorrelations become large only when compounded over multiple projection times, but should not have had a large effect on our results given the few time steps we considered. Inaccurate growth

frequency estimates over short time frames may not be a critical problem for analysis of trees. Elasticity results for our models (not presented) and for other long-lived perennial species (Silvertown *et al.* 1996) point to survivorship of large individuals as the critical determinant of population change.

Rates of demographic change were very low (i.e. few trees grew, recruited or died), resulting in population dynamics that were dominated by carryover from the previous time step. Thus, total population sizes were strongly predicted by the matrix models, but we found significant errors for some populations when we considered fractional changes to total population size. A particular problem was the Log Creek *A. magnifica* population, for which high death rates and low growth rates during the first 5-year interval were not maintained in the subsequent 5-year time steps. The reasons for this spike in mortality are not clear, although many of the dead trees were spatially clustered, suggesting a centre of infection by Annosus root rot (*Heterobasidion annosum*) (Laake 1990). The Suwanee Creek *P. lambertiana* population was also poorly predicted because of an increasing frequency of mortality caused by the ongoing effects of an introduced pathogen (van Mantgem *et al.* 2004). Size-structured models provided only marginal improvements in predictive accuracy compared with a null model and an unstructured population model. Furthermore, we found the influence of individual tree size on growth to be weak, whereas other analyses have shown tree size to be a poor predictor of survivorship in our stands (our unpublished data). Although seed production is correlated to tree size (Fowells & Schubert 1956), the rate of recruitment is likely to be heavily influenced by stand conditions. The degree to which recruitment is limited by seed input vs. site availability is not known for the Sierra Nevada, although additional data suggest that recruitment is not seed limited at our sites (P.J. van Mantgem *et al.* unpublished data). Although short-term projections were only slightly improved by including size, errors caused by not including size will be compounded over time, and longer term projections may show the inclusion of size to be increasingly important.

Spatial variance among populations appeared to be generally more important than temporal differences, with the exception of *C. decurrens*. Like other studies of herbaceous plant populations (e.g. Bierzychudek 1999), these results imply that it may be difficult to generalize the results of our population models to different sites. The Sierra Nevada is, however, topographically complex and environmental conditions are determined by a steep elevational gradient (Stephenson 1988). Elevation appears to be strongly correlated with demographic rates in our populations (Stephenson & van Mantgem in press), so it may be that demographic models of tree populations could be applied to novel populations where more uniform environmental conditions are found.

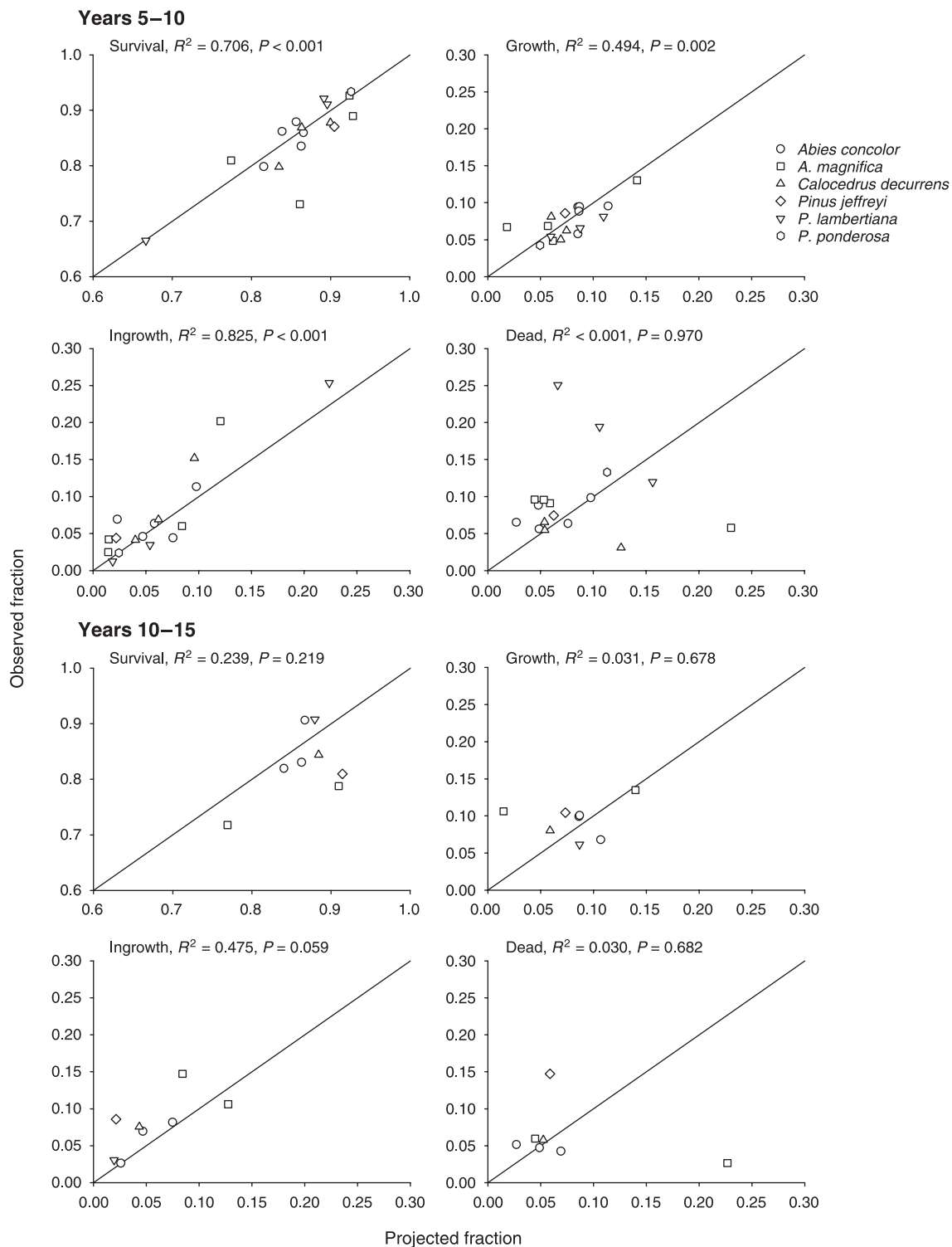


Fig. 4 Projected vs. observed vital rates for years 5–10 ($n = 17$) and 10–15 ($n = 8$). Vital rates were calculated as the fraction of individuals of the total population that experienced a particular fate. The solid line at 45° indicates perfect agreement between projected and observed fractional composition of the population. Note different scales are used for Survival.

Our time-invariant approach hinged on the temporal stability of the demographic rates. Loglinear tests demonstrated that very few populations had significant temporal variation in demographic rates, although fractional changes were sometimes highly variable (e.g. Log Creek *A. magnifica* population). One might expect that the low magnitude of temporal demographic

variability might apply to other forest tree species, for which large individuals would be buffered against small changes in environmental conditions. However, this expectation may not hold for all long-lived plants, or even all size classes of trees. For example, the small size of seedlings (individuals < 1.37 m in height) may result in their showing greater variation in growth

and survivorship rates in response to environmental changes. Likewise, density-dependent influences may be most relevant for seedlings (Silva Matos *et al.* 1999). We emphasize that the projection results considered here do not account for future events that could destabilize demographic rates. For example, prescribed fire has altered demographic rates for other populations in our forests (van Mantgem *et al.* 2004). Vital rates are also likely to change over time due to non-catastrophic fluctuations in environmental conditions (e.g. changes in stand densities). Accurately forecasting longer-term (e.g. > 25 years) population trends will almost certainly require additional data and model forms that can account for disturbance, environmental stochasticity and density dependence.

The matrix models were generally able to predict vital rates for years 5–10, although at years 10–15 the predictive ability was poorer. Model misspecifications along with small sample sizes could account for the results at years 10–15. The models did not estimate all vital rates equally well. Survival was by far the most common fate for individual trees, so it should not be surprising that our models were able to project high rates of survival accurately. Frequencies of growth and recruitment generally followed projected patterns, while death rates were more prone to errors. Tree growth and recruitment should be at least partially governed by canopy conditions, which is not likely to change drastically over short time frames in the absence of disturbance. Death rates could be influenced by longer-term environmental variations (Bigler & Bugmann 2004), so perhaps with longer observation intervals we could improve our ability to predict this rate. Alternatively, mortality may be best indicated by individual attributes other than size (Waring 1987). If true, information relevant to tree death could be difficult to capture in a traditional matrix modelling approach.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/jec/jec1007/jec1007sm.htm>

Appendix 1 Size-based projection matrices for years 0–5.

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